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# The Morphology and Relationships of the Cretaceous Teleost *Apsopelix*

SUSAN TELLER-MARSHALL

DEPARTMENT OF BIOLOGICAL SCIENCES
UNIVERSITY OF ILLINOIS AT CHICAGO CIRCLE
CHICAGO, ILLINOIS
AND
DAVID BARDACK

DEPARTMENT OF BIOLOGICAL SCIENCES
UNIVERSITY OF ILLINOIS AT CHICAGO CIRCLE
CHICAGO, ILLINOIS
AND
RESEARCH ASSOCIATE
FIELD MUSEUM OF NATURAL HISTORY

## INTRODUCTION

The fossil fishes described in this paper were first reported over a hundred years ago and have been assigned to systematic positions in different teleostean cohorts at one time or another since their discovery. Often, specimens from new localities or those preserved in an unusual manner were given new generic and specific names, adding to the confused taxonomy of these fishes. This work began as an investigation of specimens from a new locality in Texas. These specimens were preserved three dimensionally and were particularly well suited for acid preparation. Later it became evident that a complete description required examination of additional specimens and that the nomenclature of these specimens was in need of extensive revision.

*Apsopelix* was described by Cope (1871) who assigned the name to a single, fragmentary specimen (AMNH 1602) from the "Benton"

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formation (Upper Cretaceous) of Kansas. Later Cope (1875, 1877) described two other genera which he believed were similar to *Apsopelix: Syllaemus* and *Pelycorapis.* The latter genus, which contained the species *P. varius* and *P. berycinus,* was later (Dunkle, 1958) divided. *Pelycorapis varius* was assigned to *Thrissopater,* which is a synonym of *Pachyrhizodus* (Forey, 1977).

Woodward (1901, 1903, 1907) stressed the similarities among *Pelycorapis, Syllaemus, Apsopelix,* and a fourth genus, *Leptichthys* Stewart (1899). Jordan (1924) placed *Leptichthys* and *Pelycorapis* within the genus *Apsopelix* and assigned this genus to the Syllaemidae. Finally, Dunkle (1958) argued that *Helmintholepis* Cockerell (1919) and *Paleoclupea* Dante (1942) were synonyms of *Pelycorapis berycinus,* that the *berycinus* species and the *Apsopelix-Syllaemus-Leptichthys* group share "distinctive as well as general" characters. Dunkle (1958) then tentatively assigned *P. berycinus* to *Apsopelix,* the oldest available name.

Most recently, Patterson and Rosen (1977) reported that they could detect no differences between *Syllaemus, Pelycorapis berycinus, Apsopelix, Leptichthys, Helmintholepis,* and *Paleoclupea,* and treated *Apsopelix anglicus* (Dixon) as the valid name for this material. Our investigation included examination of specimens referred to *Paleoclupea, Leptichthys, Syllaemus, Pelycorapis,* and *Apsopelix,* as well as new material and supports the argument that all of these fossils represent the same fish, *Apsopelix anglicus.*

The present investigation centers on the morphology of *Apsopelix* which until now has received only cursory description. This account includes features previously undescribed and pursues in further detail features which have been inadequately considered. An attempt is made to focus on those derived characters, present in *Apsopelix,* which will permit comparison of this genus with major teleostean groups. In the past, *Apsopelix* has been assigned to the Percesoces[1] (Cope, 1875), Mugilidae (Stewart, 1900), Crossognathidae (Woodward, 1901; Patterson and Rosen, 1977), Syllaemidae (Cragin, 1901; Green, 1957), Pelycorapidae (Cragin, 1901), Clupeidae (Stewart, 1900; Woodward, 1903, 1907; Jordan, 1923; Berg, 1940), and Apsopelicidae (Romer, 1966).

*Apsopelix* is known from North America (Colorado, South Dakota, Kansas, Texas), England, and France. Part of the European material is Albian, but otherwise *Apsopelix* is restricted to the geologic interval between the Cenomanian and Santonian, possibly

Campanian (but see p. 4) stages of the Upper Cretaceous. It is a unique fish. The antorbitals, scales, and pelvic bones are larger than those in other teleosts of comparable size. The cranial roofing bones are distinctive, and the maxilla comprises nearly all of the dermal upper jaw. Thus, specimens of *Apsopelix* are easily recognized. The combined advantages of three-dimensional preservation of some fossil material and of acid preparation techniques have facilitated a complete account of the skull. Remaining specimens elucidate most of the post-cranial skeleton, but the caudal skeleton is not complete in any specimen examined. This incomplete preservation of the caudal skeleton is characteristic of *Apsopelix,* but enough information is available from these specimens to permit some conclusions about the caudal morphology.

The morphological adaptations of *Apsopelix* include features associated with microphagous feeding, particularly the long gill rakers. The gut must have been very long, judging from the remote position of the anal fin. The body was more robust than laterally compressed. These clues indicate that the diet was probably in large part comprised of material difficult to digest, such as plankton.

## ACKNOWLEDGEMENTS

For information concerning *Apsopelix* we thank Peter L. Forey and Colin Patterson, British Museum of Natural History; and Donn E. Rosen, American Museum of Natural History.The drawings were prepared by Karen Baker Al Lerio and the manuscript typed by Mrs. Beverly Woodard.

## SPECIMENS EXAMINED

Material from several museums has been prepared and studied. Abbreviations include: AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; KU, University of Kansas Museum of Natural History; SMM, Sternberg Memorial Museum; USNM, United States National Museum; UT, University of Texas Vertebrate Paleontological Collections.

[1]The suborder Percesoces was once used to unite the Crossognathidae, Ammodytidae, Scombresocidae, Atherinidae, Mugilidae, and Sphyraenidae. See Woodward, 1901, Part IV, p. 347 for diagnosis.

AMNH 1602, fish body

FMNH PF7463, three-dimensional head and anterior of body, Eagle Ford Formation, Dallas County, Texas, Texas Industries Quarry, southwest of intersection of Chalk Hill Road and Dallas-Ft. Worth Turnpike.

KU 309, whole fish; KU 310, fish without tail; KU 318, head and pectoral girdle; KU 519, whole fish, Smoky Hill Chalk Member, Niobrara Formation, western Kansas.

KU 18, fish without tail, Fencepost Limestone Bed at top of Greenhorn Formation, western Kansas.

KU 882, three-dimensional head and anterior of body, Jetmore or Lincoln limestone levels of Greenhorn Formation, Mitchell County, Kansas, 1 mile northeast of Scotsville.

SMM 7958, whole fish, Smoky Hill Chalk Member, Niobrara Formation, Kansas.

USNM 16725, three-dimensional head and anterior part of body, Pierre Shale, Chamberlain, South Dakota (as per catalogue, but horizon and location uncertain as there is no evidence of the matrix similar to that containing the fossil at this location.)

UT 848, posterior part of head and anterior part of body, Upper Cretaceous (horizon uncertain), Williamson County, Texas, 1¾ miles east of Coupland in branch of Bushy Creek.

UT 31051-7, whole fish, Austin Group, Ector Member, Fannin County, Texas, Savoy Pit 4 miles south of Savoy on farm road 1752, then east three-quarters of a mile on unpaved road.

UT 40092-6, whole fish, basal Austin Chalk, Grayson County, Texas west of farm road 1417 where it passes radar tower of Perry AFB.

## SYSTEMATIC DESCRIPTION

### Subdivision Teleostei (sensu Patterson, 1975)
### Order incertae sedis
### Family Crossognathidae Patterson and Rosen, 1977

### Genus **Apsopelix** Cope, 1871

*Apsopelix* Cope, 1871, p. 424; Jordan, 1924, p. 230, pl. XX; Dunkle, 1958, p. 271. Type species: *A. sauriformis* (monotypy).

*Syllaemus* Cope, 1875, p. 180; Stewart, 1900, p. 384, pl. LXXII fig. 2; Woodward, 1901, p. 350; Cragin, 1901, p. 26, pl. I; Woodward, 1903, p. 88, pl. XX, pl. XXI figs. 1-2; Chabanaud, 1930, p. 646, pl. LXVIII; Green, 1957, p. 40, figs. 1-2; Wenz, 1965, p. 13, figs. 3-5, pl. II. Type species: *S. latifrons* (monotypy).

*Pelycorapis* Cope (not Cope, 1874), 1877, p. 587. Type species: *Thrissopater varius* (monotypy).

*Leptichthys* Stewart, 1890, p. 78; Stewart, 1900, p. 372, pl. LXXII fig. 1; Jordan, 1924, p. 231, pl. XXI. Type species: *L. agilis* (monotypy).

*Helmintholepis* Cockerell, 1919, p. 176, pl. XXXII, fig. 4. Type species: *H. vermiculatus* (monotypy).

*Paleoclupea* Dante, 1942, p. 340, figs. 1-4. Type species: *P. dakotensis* (monotypy).

*Diagnosis.*—Teleost fishes in which the trunk is fusiform, and head length about equal to greatest depth. Head tapers ventrally. Orbit diameter 25-30 per cent head length, nearly equal in length to ethmoid region; sclerotic ring ossified, snout pointed. Rostral fused with underlying mesethmoid, shield-like anteriorly with paired splints passing back below frontals. Cranial roof arched transversely with a median depression where frontals meet parietals; parietals wider than long, medially united. Roofed posttemporal fossae confluent above cranial vault, extending forward to orbitosphenoid; deep dilatator and subtemporal fossae; orbitosphenoid forms vertical plate across upper third of orbit; basisphenoid present; parasphenoid forms angle at ascending wings and extends posteriorly beyond braincase. Occipital condyle formed by basioccipital and exoccipitals. Hyomandibular vertical with posteriorly directed fossa below neurocranial head. Palate with ossified processes which meet lateral and median ethmoid elements. Lower jaw articulation lies beneath anterior third of orbit. Premaxilla about one-tenth of upper jaw; maxilla arcuate, about eight times longer than maximum depth; two supramaxillae. Coronoid height of mandible contained 2½ times in mandible length. Angular and articular fused, retroarticular distinct. Parasphenoid toothless. Basihyal with a pair of tooth plates; gill rakers long and slender. No bone-enclosed ethmoid commissure; preopercular and infraorbital sensory canals with short, bone-enclosed branches; lateral line conspicuous. Dermosphenotic and supraorbitals large; antorbital nearly covers ethmoid region; posterior infraorbitals extend to preopercular, no suborbitals. Preopercular expanded ventroposteriorly with radiating ridges on expanded surface; operculum and suboperculum smooth, about equal in size. Scales cycloid, 10-12 rows on one side at midbody; height of exposed portion of each scale about twice its length. About 40 preural centra, about 12 caudal centra; each centrum with a single lateral ridge, neural arches fused to all but anterior centra; epineural, epipleural, and epicentral intermusculars present. Pectoral fins with about 15 rays; pelvic fins abdominal with at least 12 rays, pelvic bone broadly expanded. Dorsal fin with at least 13 rays, originating about midway between snout and posterior end of body; anal fin short and very close to caudal origin; caudal fin deeply forked with narrow

base; fin rays cross hypurals at steep angle. Uroneurals modified posteriorly, anterior uroneurals cover lateral faces of ural and first two preural centra.

### Apsopelix anglicus (Dixon)

*Calamopleurus*[1] *anglicus* Dixon, 1850, p. 375, pl. XXXII, figs. 11-12.

*Apsopelix sauriformis* Cope, 1871, p. 424; Jordan, 1924, p. 230, pl. XX; Dunkle, 1958, p. 271.

*Syllaemus latifrons* Cope, 1875, p. 181; Stewart, 1900, p. 384, pl. LXXII, fig. 2; Woodward, 1901, p. 351; Cragin, 1901, p. 27, pl. I.

*Pelycorapis berycinus* Cope, 1877, p. 587.

*Calamopleurus anglicus* Woodward, 1888, p. 324.

*Leptichthys agilis* Stewart, 1899, p. 78; Stewart, 1900, p. 372, pl. LXXII, fig. 1; Jordan, 1924, p. 231, pl. XXI.

*Syllaemus anglicus* Woodward, 1901, p. 351; Woodward, 1903, p. 89, pl. XX, pl. XXI figs. 1-2; Chabanaud, 1930, p. 646, pl. LXVIII.

*Helmintholepis vermiculatus* Cockerell, 1919, p. 176, pl. XXXII, fig. 4.

*Paleoclupea dakotensis* Dante, 1942, p. 340, figs. 1-4.

*Syllaemus hanifii* Green, 1957, p. 40, figs. 1-2.

*Syllaemus albiensis* Wenz, 1965, p. 13, figs. 3-5, pl. II.

*Diagnosis.*—As for genus, only species. Proportions (as a percentage of standard length): head length 23-25, greatest depth 23-25, prepectoral 28-29, prepelvic 71-75, predorsal 41-42, preanal 81-83.

*Description.*—

GENERAL FEATURES: The head is triangular in lateral view with the posterior border being gently curved. Dorsally the head forms a relatively broad, flat surface and tapers ventrally. Maximum head depth behind the lower jaw articulation equals about 65 per cent of the head length. Diameter of the orbit is slightly less than the preorbital distance and represents about 30 per cent of the head length. The jaw articulation lies beneath and slightly anterior to the middle of the orbit. Three specimens preserved in three-dimensional form probably closely retain the original shape of the fish. Examination of these suggests that the body was deeper than wide, ovoid in cross-section (at least at mid-body), and somewhat wider ventrally than dorsally. Scales with their exposed area twice as high as long cover the body. Both the pectoral and pelvic fins insert ventrally.

[1]*Calamopleurus* was founded by Agassiz on fragments of an entirely different fish from the Upper Cretaceous of Brazil. See Woodward, 1903, p. 89.

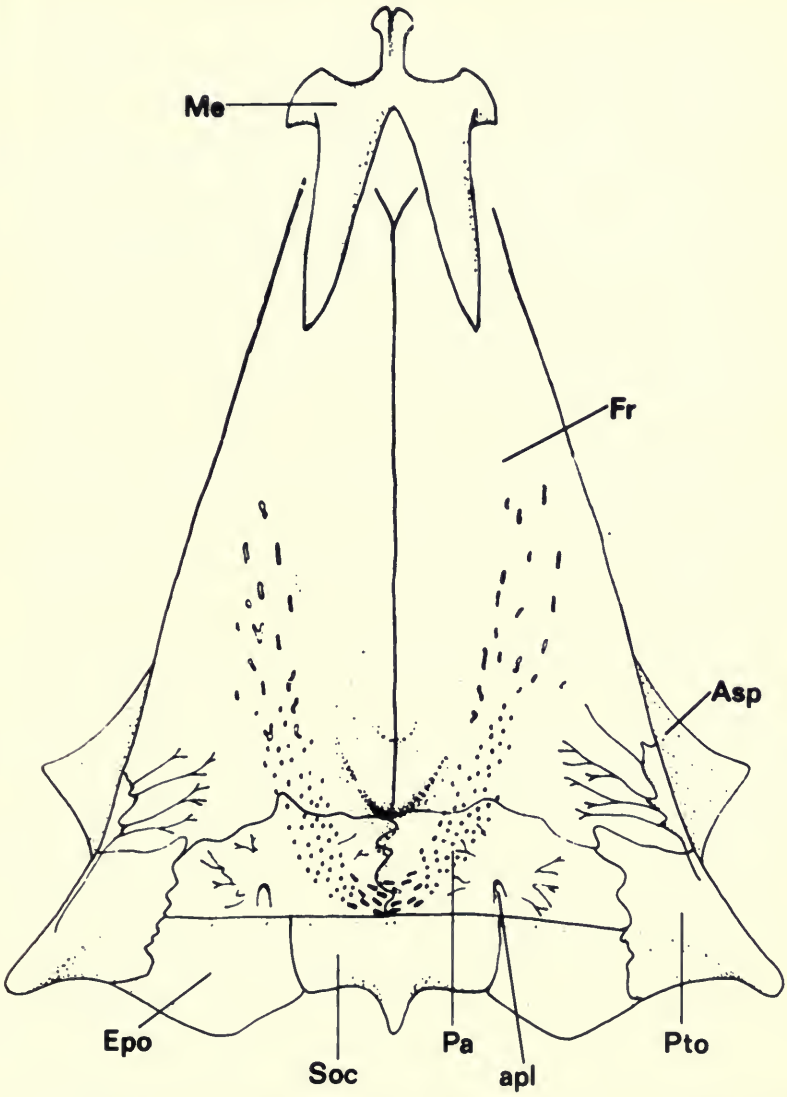


FIG. 1. *Apsopelix anglicus*, dorsal view of the neurocranium. For abbreviations see p. 30.

Pelvic fins are abdominal, the dorsal and anal fins are short. The caudal fin is slender and deeply forked.

NEUROCRANIUM (figs. 1-5): The neurocranium is 2½ times as long as deep; its maximum width across the pterotics equals nearly

three-fourths the total neurocranial length. The postorbital part of the braincase is short, accounting for less than one-third of the total neurocranial length. Maximum neurocranial depth occurs just behind the orbit.

The posttemporal fossae (fig. 3, ptf), subtemporal fossae (fig. 3, stf), and dilatator fossae (fig. 3, df) are well developed. The posttemporal fossae are confluent above the cranial vault and extend well forward, probably to the orbitosphenoid. As in megalopids, the vertical depth of these fossae has resulted in a pronounced convexity of the skull roof in the otic region. In posterior view (fig. 4) the neurocranium slopes ventrolaterally from the midline so that its dorsal surface describes an arc of 130° around an axis at the middle of the basioccipital.

The frontals (fig. 1, Fr) are flat sheets of bone, narrow anteriorly, then widening gradually to contact the parietals and pterotics posteriorly. The frontals are joined by a straight suture and form a median depression in the cranial roof (fig. 1) just anterior to the fronto-parietal juncture. Each frontal shows a line of irregularly shaped ridges and pits marking the path of the supraorbital sensory canal. These lines diverge anteriorly.

The parietals (figs. 1-2, Pa) meet in the dorsal midline at a wavy suture. They are wider than long and taper laterally, extending more than half the distance from their joint suture to the lateral edge of the cranial roof. They are also marked with ridges and pits, including a prominent, centrally located pit line (fig. 2, apl).

Each pterotic (figs. 1-4, Pto) forms the dorsolateral corner of the neurocranium and makes up the lateral wall plus part of the dorsal and ventral walls of the posttemporal fossa. In dorsal view the dermopterotics meet the frontal, parietal, and epioccipital with irregularly shaped sutures. The lateral surface of the autopterotic is deeply excavated to form, along with the autosphenotic, the dilatator fossa. This fossa is roofed by the frontal and more posteriorly by a lateral extension of the dermopterotic. Beneath this fossa, the hyomandibular facet (fig. 3, fhm) slopes anteroventrally and continues forward onto the autosphenotic. The facet is slightly constricted midway along its length. Beneath the hyomandibular facet is a deep subtemporal fossa (fig. 3, stf), its long axis sloping anteroventrally. The autopterotic forms the roof of this fossa.

The epioccipitals (figs. 1, 4, Epo) are visible in dorsal and posterior views. They contact the parietals anteriorly, the supraoccipital

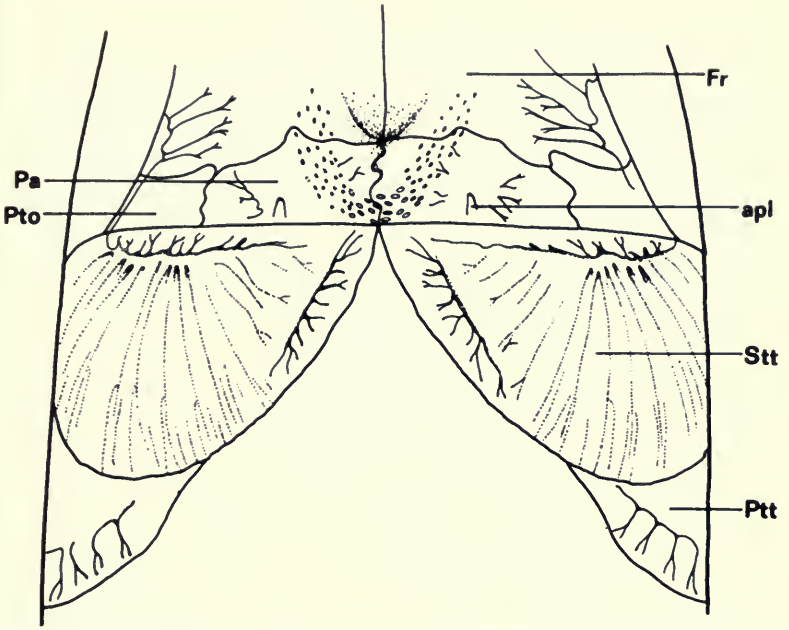


FIG. 2. *Apsopelix anglicus*, dorsal view of the posterior third of the neurocranium. For abbreviations see p. 30.

medially, and the pterotics laterally. The dorsal surface of each epioccipital tapers and is produced posteriorly over the dorsomedial corner of the posttemporal fossa. The epioccipitals are covered dorsally by large supratemporals (fig. 2, Stt). A transverse groove along the anterior margin of the epioccipitals and supraoccipital marks the line of contact between the supratemporals and neurocranium. In posterior view the epioccipitals contact the supraoccipital medially and the exoccipitals ventrally. In this view they are square-shaped, with the lateral margin and ventrolateral corner thickened to form a rounded ridge (fig. 4). This ridge continues onto the exoccipital. The epioccipitals contribute to the dorsomedial and most of the medial wall of the posttemporal fossa.

The supraoccipital (figs. 1, 4, Soc) is visible in dorsal and posterior views. Dorsally it is wider than long and exhibits a small, median, posteriorly directed prong. In posterior view it is pentagonal, and about as deep as wide. Together with the exoccipitals, the supraoccipital is gently concave in posterior view.

The exoccipitals (figs. 3, 4, Exo) each exhibit a triradiate set of

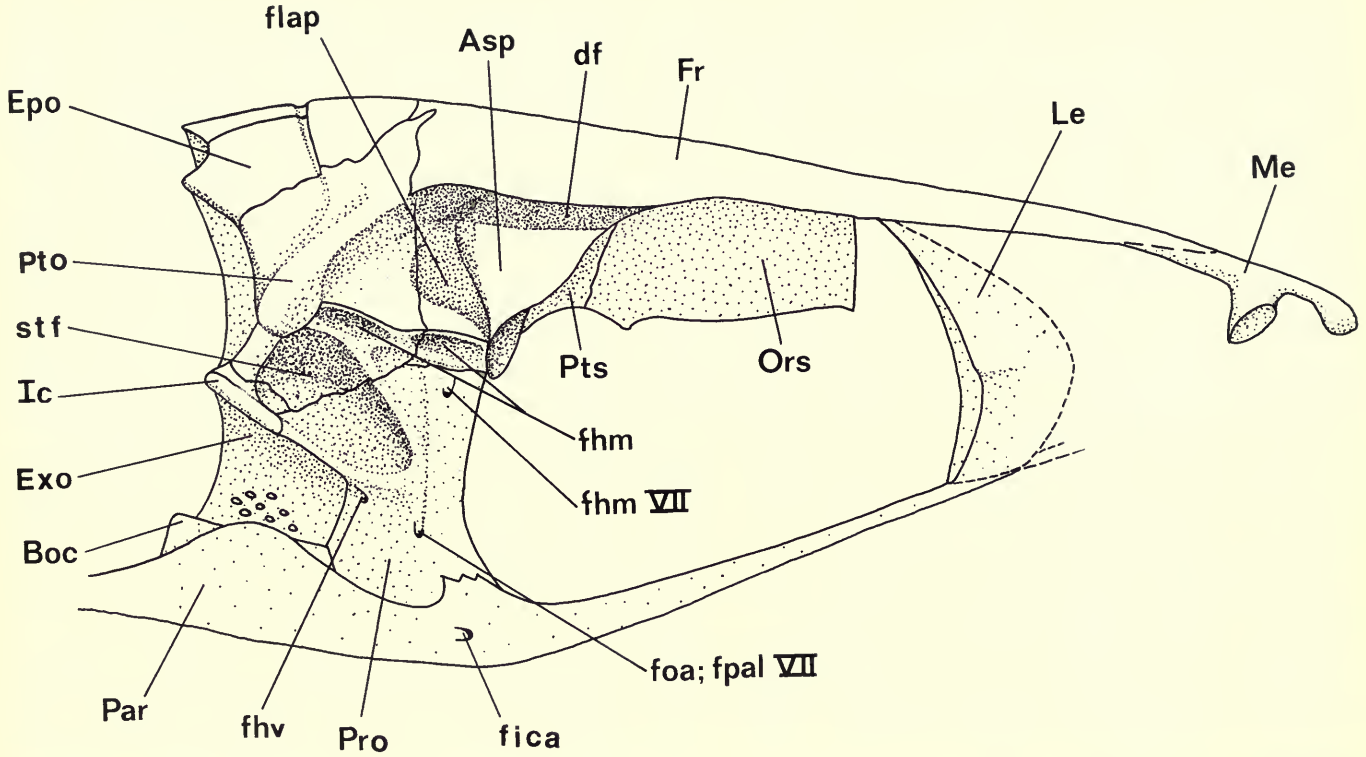


FIG. 3. *Apsopelix anglicus*, lateral view of the neurocranium. For abbreviations see p. 30.

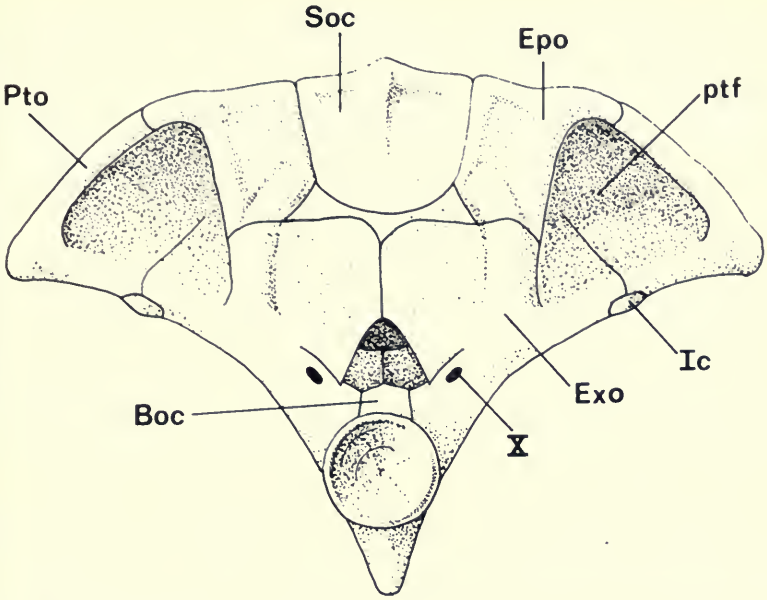


FIG. 4. *Apsopelix anglicus*, posterior view of the neurocranium. For abbreviations see p. 30.

rounded ridges in posterior view. The dorsally directed ridge is sutured to a ventrolaterally thickened arm of the epioccipital. The laterally directed ridge meets the intercalar and autopterotic where these bones form the floor of the posttemporal fossa, while the ventromedially directed ridge contacts the basioccipital and contributes to the occipital condyle. Lateral to the foramen magnum is the foramen for the vagus nerve trunk (fig. 4, X), while the glossopharyngeal nerve trunk probably emerged through one of the numerous foramina on the posterolateral surface of the exoccipital (fig. 3); the remainder of these foramina probably carried blood vessels and the supratemporal branches of IX and X.

The intercalars (figs. 3, 4, Ic) are small and barely visible in posterior view. Each does, however, extend forward to meet the prootic along the margin of the subtemporal fossa.

The basioccipital (figs. 3, 4, Boc) lies beneath the exoccipitals and is covered laterally by the parasphenoid. In lateral view the surface of the basioccipital is concave. These depressions may have housed anterior extensions of the swimbladder.

The prootics (fig. 3, Pro) are deeper than long in lateral view and

expanded dorsally to meet the autopterotics, autosphenotics, and pterosphenoids. Ventrally each prootic forms a thin sheet overlapped laterally by ascending wings of the parasphenoid. There is a slender, posteriorly directed arm which forms the ventroposterior wall of the subtemporal fossa and contacts the intercalar, while the main body of the prootic contributes to the anterior wall of this fossa. Ventral to the base of this posteriorly directed arm is the foramen for posterior exit of the lateral head vein (fig. 3, fhv). More anteriorly on the lateral surface of the prootic are two additional foramina for the orbitonasal artery and palatine branch of VII (fig. 3, foa; fpal VII) and for the hyomandibular branch of VII (fig. 3, fhm VII). The anterior surface of the prootic shows a triangular pattern of foramina of equal size; two lateral foramina mark the exit of the trigeminal nerve and the anterior exit of the lateral head vein, while the more medial foramen marks the exit of the oculomotor nerve.

The autosphenotics (fig. 1, 3, Asp) are triangular in dorsal view, rectangular in orbital view, and produced laterally to a prominent spine. The dorsal and posterior surfaces are concave, while the orbital surface is nearly flat and vertical. This latter face is pierced by a foramen for the otic branch of the facial nerve. Behind the spine a pocket on the posterior face of the autosphenotic (fig. 3, flap), oriented more ventrally than horizontally, probably marks the origin of part of the levator arcus palatini (cf. Forey, 1973a, p. 1,308). The dorsal surface of the autosphenotic contributes to the dilatator fossa (fig. 3, df).

The pterosphenoids (fig. 3, Pts) are anteriorly facing sheets which form the margin of the optic foramen with their medial edges. Lateral and dorsal to the optic foramen is a small opening within each pterosphenoid probably for the trochlear.

The orbitosphenoid (fig. 3, Ors) extends forward in front of the pterosphenoids. It is a vertical sheet of bone longer than deep and extending more than half the distance to the anterior margin of the orbit. The dorsal part of this sheet is enlarged where the olfactory tract lay, and a foramen at the anterior end of the bone marks the exit of this tract.

The basisphenoid is Y-shaped in orbital view; the upper arms of the Y form a gentle yolk shaped edge, and the vertical stem of the Y is longer than the arms. The stem contacts the parasphenoid below, while the arms touch the prootics and pterosphenoids above.

The parasphenoid (fig. 3, Par) forms an obtuse angle beneath its

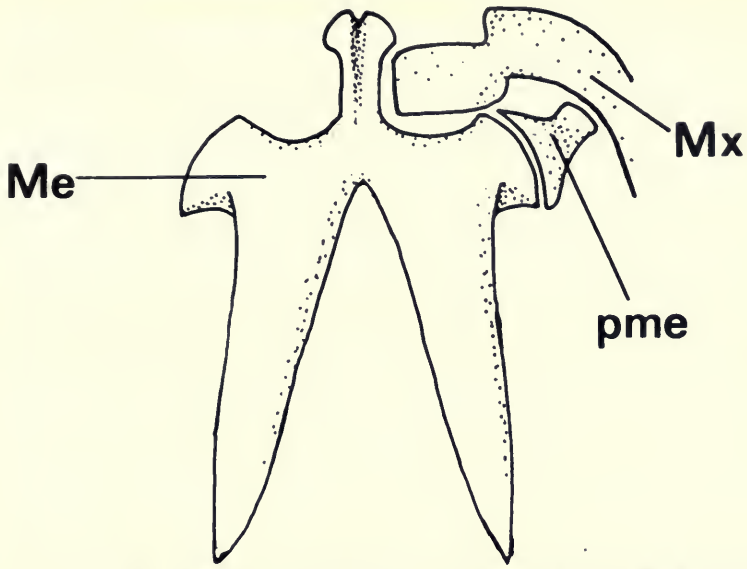


FIG. 5. *Apsopelix anglicus*, dorsal view of the ethmoid region showing the relationships of the median ethmoid (Me), palatine process (pme), and maxilla (Mx). For abbreviations, see p. 30.

junction with the prootic. Anteriorly it is a slender, triangular strut deeply cleft for receipt of the vomer. Behind the point where the ascending wings of the parasphenoid meet the prootics, the parasphenoid deepens, increasing the size of the posterior myodome, and extends ventrally as an elongated process which passes beneath and posterior to the basioccipital. The parasphenoid appears to be toothless.

The ethmoid region is well ossified. It consists of a single dorsal median ethmoid (figs. 1, 5, Me), probably the result of fusion between a smooth dermal rostral and the underlying peri and endochondral ossifications (see Patterson, 1970 for a discussion of the ethmoid region and Nelson, 1969, p. 8 regarding use of the word "fusion"). There is a narrow ventral vomer and a pair of stout lateral ethmoids (fig. 3, Le) which form the anterior boundary of the orbit.

The posterior extent of the vomer could not be determined directly; however, KU 882 shows a ventral cleft between anterior arms of the parasphenoid presumably occupied by the vomer. This cleft disappears beneath the middle of the orbit, but it was filled by matrix posteriorly so that it is likely that the ossified vomer extended only as far as the posterior edge of the ethmoid region. Patterson

and Rosen (1977) cite a partially paired vomerine tooth patch in *Apsopelix*, but none of the specimens examined in this study show evidence of vomerine teeth.

The median ethmoid bifurcates posteriorly, each half tapering beneath the frontals. Anterior to the bifurcation the ethmoid widens, extending anteroventrally to abut on either side against a dorsally directed process from the palatine (figs. 5-6, pme). The most anterior part of the ethmoid is narrow and biconcave to receive the anterior ends of the maxillae. There is no evidence of a bone enclosed ethmoid commissure.

The lateral ethmoids are set back some distance from the median ethmoid since the ethmoid region at least equals the orbit in length. Anteriorly, the lateral ethmoid forms the posterior wall of the nasal capsule, then increases in depth toward the orbit, spanning the distance between the frontal above and the parasphenoid below. A small depression on the posterior surface of the lateral ethmoid, at the ventrolateral corner, receives a dorsal process from the palate (fig. 6, ple).

HYOPALATINE SERIES (figs. 5-7): Elements of the hyopalatine series are similar in their relationships to those of other lower teleosts, but some of the bones have distinct characteristics. Each hyomandibular (fig. 6, Hm) is vertical with an expanded neurocranial head. The narrow shaft has a groove along its anterior edge. The medial side of this groove extends forward as a thin sheet of bone. Just below the neurocranial head is a large posterior fossa which contained the origin of the dilatator operculi. In front of this fossa are numerous small foramina.

Forey (1975, pp. 170-172, fig. 12) has contrasted the hyomandibular architecture and muscle origins in *Elops* and two clupemorphs. As far as the levator arcus palatini and the dilatator operculi are concerned, the skeletal features of *Apsopelix* indicate that the muscle arrangements probably differed from that in *Elops* and other early teleosts. But the arrangement of these muscles in *Apsopelix* was not as in clupeomorphs either, since in *Apsopelix* the dermosphenotic is large, there is no ridge on the frontal, and no anterodorsal process on the hyomandibular (cf. Forey, 1975, fig. 12b).

In *Apsopelix* there appears to have been a shift of at least part of the dilatator operculi to an origin on the hyomandibular, freeing the posterior edge of the autosphenotic for origin of levator arcus

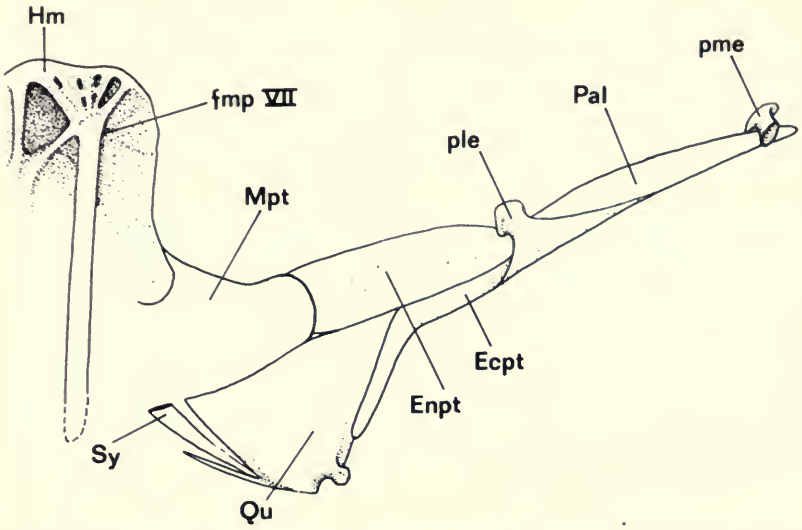


FIG. 6. *Apsopelix anglicus*, right hyopalatine series in lateral view. For abbreviations see p. 30.

palatini fibers in order to meet the demands of a microphagous feeding mode that requires complex movements and increased efficiency of the palate abductors. So, while both *Apsopelix* and clupeomorphs exhibit morphological adaptations associated with the microphagous feeding mode, the adaptations of *Apsopelix* differ from those of clupeomorphs and are not indicative of a close relationship.

Between the shaft and the anterior bony sheet of the hyomandibular are two foramina, one of which probably marks the exit of the mandibular and preopercular branches of the facial nerve (fig. 6, fmp VII).

The metapterygoid (fig. 6, Mpt) is an elongate bone, saddle-shaped where its anterior edge overlaps the endopterygoid (fig. 6, Enpt). Posteriorly the metapterygoid joins the lower portion of the hyomandibular, but the suture is difficult to follow. The ventral edge of the metapterygoid lies along the dorsal border of the quadrate. Each ectopterygoid (fig. 6, Ecpt) is boomerang-shaped and lies along the anterior edge of the quadrate. It then curves anteriorly, continuing along the lateral edge of the endopterygoid (fig. 6, Enpt). None of the pterygoid elements appear to bear dentition.

The anterior part of the palate shows no sutures on the specimens examined and there is some difficulty determining whether the lateral ethmoid process of the palate (fig. 6, ple) stems from the posterior part of the palatine as in *Albula vulpes* (Forey, 1973b, fig. 79) or from the anterior part of the ectopterygoid as in *Clupea harengus* (Kirchoff, 1958, figs. 11, 15, 16).

The palatine (fig. 6, Pal) is well ossified throughout its length and bears an anterior process (figs. 5-6, pme) which extends between the median ethmoid and the maxilla. This process is fused to the palatine in FMNH PF7463. It appears to be a separate ossification in USNM 16725, but it is intimately associated with the dermopalatine and is not an ethmoid element (cf. Wenz, 1965, fig. 3). This same process is an ossification of the autopalatine in *Albula vulpes*. SMM 7958 shows a number of conical teeth on the palatine; these teeth are larger than the similarly shaped teeth on the jaw elements.

The quadrate (fig. 6, Qu) is broadly expanded dorsally to meet the pterygoids. Posteriorly it bears a deep, broad notch for the symplectic (fig. 6, Sy). The quadrate condyle lies beneath the orbit. Behind the condyle a notch in the quadrate receives the postarticular process of the angular (fig. 7).

UPPER JAW (figs. 5, 8): The upper jaw consists of a premaxilla, maxilla, and two supramaxillae. A premaxilla has never been described in *Apsopelix*. Of the specimens examined in this study only one, KU 18, retains a fragment of it. A small, laminar bone, it bears minute acuminate teeth. The premaxilla probably fits into a notch at the anterior end of the maxilla (fig. 5), but its true extent and shape remain unknown.

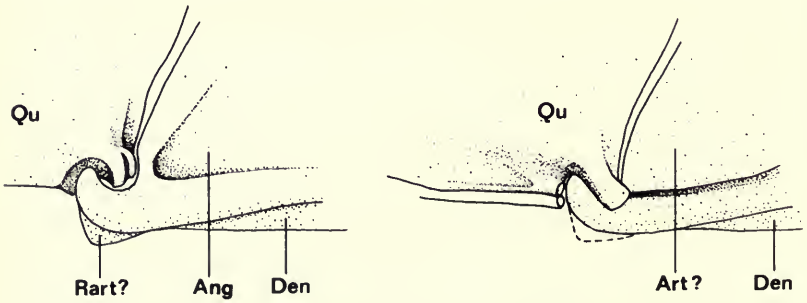


FIG. 7. *Apsopelix anglicus* lateral (left) and medial (right) views of the lower jaw articulation. For abbreviations see p. 30.

The maxilla (figs. 5, 8, Mx) extends from beneath the anterior end of the orbit forward to articulate with the median ethmoid. It is a sabre-shaped bone, nearly uniform in depth throughout its length, and about 12 times longer than deep. Dentition consists of a single row of minute marginal teeth similar to those on the premaxilla, 0.5 mm. from base to tip in FMNH PF 7463.

The anterior supramaxilla (fig. 8, Smx 1) is the longer of the two. Neither of these bones bears an anterior projection as in many other lower teleosts, but rather the posterior supramaxilla barely overlies its anterior partner. UT 31051-7 is preserved with the mouth open and shows that the supramaxillae do not separate as much as in clupeoids, but tend to function as a unit. Both supramaxillae exhibit rugose ornamentation along their entire length and are as deep as the maxilla at their deepest point.

LOWER JAW (figs. 7-8): The lower jaw is short and deep. Maximum depth is between one-third and one-half total length and occurs about midway along this length. The ventral margins of both the dentary (figs. 7-8, Den) and angular (figs. 7-8, Ang) curve medially to form a narrow shelf marked with pores for the mandibular sensory canal. The number of these pores is uncertain, but there appear to be at least two on the posterior part of the dentary and one on the angular. Mandibular dentition consists of a single row of minute teeth, like those on the maxilla, along the dentary margin.

The dentaries meet in a short anterior symphysis without curving much inward. Each dentary receives the angular in a deep posterior notch and extends back above and below it (fig. 7). A postarticular process of the angular extends behind the facet for the quadrate condyle, although this structure is broken off easily and is missing in all but one of the specimens examined, KU 318.

There is a small, distinct retroarticular visible in KU 318, USNM 16725, and UT 40092-26. Whether this element takes part in or is excluded from the articular facet could not be determined from these specimens. The medial surface of the angular shows a pocket filled by what appears to be an articular in KU 318 (fig. 7, Art). Patterson and Rosen (1977) state that in BMNH 47302 the mandibular sensory canal opening is in the medial position, the angular and articular are fused, and the retroarticular is free except on the surface of the facet for the quadrate where all three bones appear to be fused.

HYOID AND BRANCHIAL ARCHES: Some elements of the hyoid and branchial arches are preserved in FMNH PF 7463, including one anterior ceratohyal, hypohyals, basihyal, the anterior epibranchials and ceratobranchials, one hypobranchial, and one basibranchial. The anterior ceratohyal is rectangular with a gently concave ventral edge and a centrally located foramen. Two equally developed hypohyals meet the anterior edge of the ceratohyal.

The basihyal ossified only posteriorly. A pair of tooth plates lies on its oral surface and extends forward beyond the ossified element. Each tooth plate is about one-fifth as wide as long and covers the lateral third of the basihyal, leaving the center of that bone without teeth. There are 10 longitudinal rows of small, posteriorly directed tooth bases per tooth plate. The basihyal is the only element of the hyoid series with dentition preserved. Along the oral edge of the epibranchials and ceratobranchials are a series of gently curved gill rakers, about 8 mm. in length. There are no tooth plates present on any of the branchial arches.

Impressions of 12 branchiostegal rays are present in UT 31051-7, but the irregular nature of the spaces between these grooves indicates that there were more rays.

DERMAL BONES OF THE CHEEK (fig. 8): The infraorbitals are preserved in FMNH PF 7463 and USNM 16725. There is a large antorbital followed by at least three distinct infraorbitals plus a dermosphenotic. The postorbital components of this series extend back as far as the preoperculum.

The antorbital (fig. 8, Ao) is wedge shaped, expanded posteriorly, and tapering to a blunt anterior edge. There are two anteroposteriorly oriented grooves on the antorbital, the lower probably associated with the infraorbital sensory canal as it entered the antorbital, while the more dorsal probably housed the antorbital branch of that canal. The dorsal edge of the antorbital overlaps the first supraorbital.

The infraorbitals are so fragmented that it is difficult to determine their exact number. The primitive condition of the teleostean infraorbital series probably included seven separate bones from the antorbital to the dermosphenotic (Nelson, 1969). There appears to have been a reduction in the number of infraorbital bones in *Apsopelix*. However, there is some question as to where the implied fusion has occurred. Wenz (1965, fig. 5, p. 18) figured *Apsopelix* with an antorbital plus five infraorbitals, including the dermosphenotic.

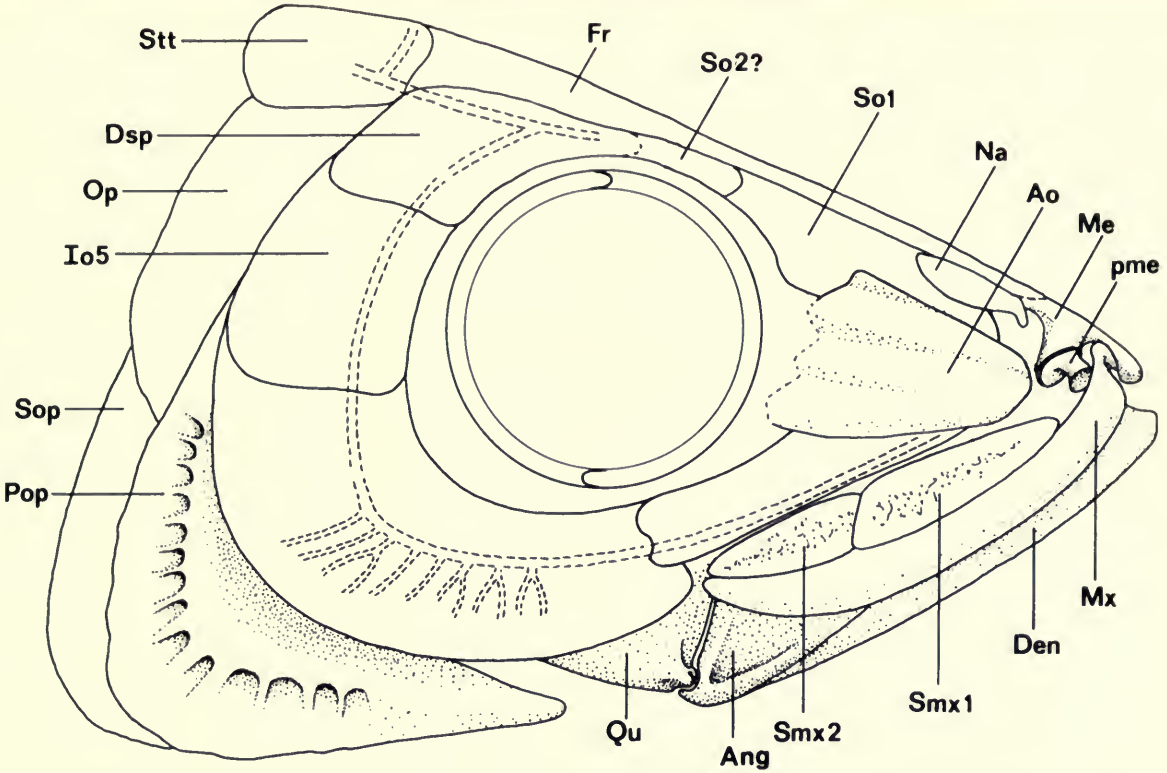


FIG. 8. *Apsopelix anglicus*, restoration of head in right lateral view. For abbreviations see p. 30.

There is a large infraorbital covering the posteroventral region of the cheek and marked by several branches of the infraorbital sensory canal. Above this largest bone in the series are figured two more bones plus the dermosphenotic, implying that the large bone is a fusion of the infraorbitals 2 + 3.

In USNM 16725 and FMNH PF 7463, the large infraorbital covering the posteroventral area of the cheek and marked by branches of the infraorbital sensory canal is easily recognized, but there appears to be only one additional bone (fig. 8, Io5) between the large infraorbital and the dermosphenotic, implying that the large element is a fusion of Io 2 + 3+4. If Wenz's (1965) interpretation is correct, then it is possible that the element referred to in our paper as Io5 is actually a fusion of Io 4+5.

The dermosphenotic is an elongate, triangular bone overlying the autosphenotic and covering the dilatator fossa. It is smooth where it meets the infraorbitals, but ornamented with ridges and pits where it contacts the frontal. This ornamentation marks the meeting of the temporal and infraorbital canal. The infraorbital sensory canal traverses a path through the center of the infraorbital bones.

There is at least one long, anteriorly expanded supraorbital (fig. 8, SO 1) and possibly a second, smaller supraorbital evident only in USNM 16725. The first supraorbital covers the anterior margin of the orbit posteriorly and extends forward medial to the antorbital. The second supraorbital (fig. 8, SO 2) spans the distance between the posterior edge of the first supraorbital and the anterior edge of the dermosphenotic.

The nasal is a small, rod-shaped bone (fig. 8, Na) above and anterior to the first supraorbital in USNM 16725. It is in line with the anterior part of the supraorbital sensory canal on the frontal and shows evidence of a bone enclosed canal. The nasals appear to taper anteriorly, but this could be an artifact of preservation.

OPERCULAR SERIES (fig. 8): The preoperculum (fig. 8, Pop) expands ventrally from a relatively narrow dorsal end. The surface of the expanded portion is marked by radiating ridges which end posteriorly as fine lines, each ridge giving rise to about four lines. Pores of the preopercular sensory canal are evident along the anterior margin of these radiating ridges. The sensory canal does not run along the anterior margin of the bone, but rather through its center, particularly at the angle (cf. Forey, 1973b, *Elops,* fig. 6, p. 19).

The operculum (fig. 8, Op) is smooth and without ornamentation. Its width is contained in its length 1⅓ times. It has a gently curved posterior border, and is barely overlapped anteriorly by the preoperculum. The suboperculum (fig. 8, Sop) is also smooth and about the same size and shape as the operculum. Most of its surface is covered by the expanded ventral portion of the preoperculum. The interoperculum is covered by the preoperculum except for its ventral edge. It is about as long as the suboperculum.

SCALES (fig. 10): The scales are large and cycloid. Faint anteroposteriorly oriented folds and closely spaced circuli are visible on the exposed surface. A complete scale is longer than deep, the deepest portion being posterior to the center. There are 10-12 longitudinal rows of scales present on each side. The sixth transverse row from the dorsal fin carries the lateral line, which consists of a series of simple tube-like openings. Dunkle (1958, pp. 269-270) discussed the scales of *Apsopelix* in detail.

PAIRED FINS AND THEIR SUPPORTS (figs. 2, 9, 10): The paired fins are in the primitive position for teleosts, the pectorals inserting low on the flank and the pelvics set back in the abdominal region. There are at least 15 rays on the broad-based pectoral fins and at least 12 rays on the pelvic fins (fig. 10).

The supratemporals (fig. 2, Stt) are scale-like sheets of bone which overlap the supraoccipital, epioccipitals, and pterotics in dorsal view. Their anterior surface has coarse rugae which follow the path of the supratemporal commissure and its posteriorly directed branches. The supratemporals meet only at their anterior edges on the dorsal midline.

The posttemporals (fig. 2, Ptt) and supracleithra are rod-shaped bones. The supracleithrum is longer than the posttemporal. The lateral line traverses the posttemporal near its posterodorsal margin along the anterior half of its length. The supracleithrum overlaps a considerable portion of the cleithrum, and reaches the level of the ventral margin of the orbit ventrally.

Each cleithrum curves anteroventrally and medially around the gill chamber and meets its complement in the ventral midline just anterior to this chamber. The lateral surface of the cleithrum is expanded above the pectoral fin and there appears to be at least one scale-like postcleithrum just above the pectoral fin base.

Only the posterior end of the scapula has been observed; it has a rounded ridge which forms a point of attachment for the first pec-

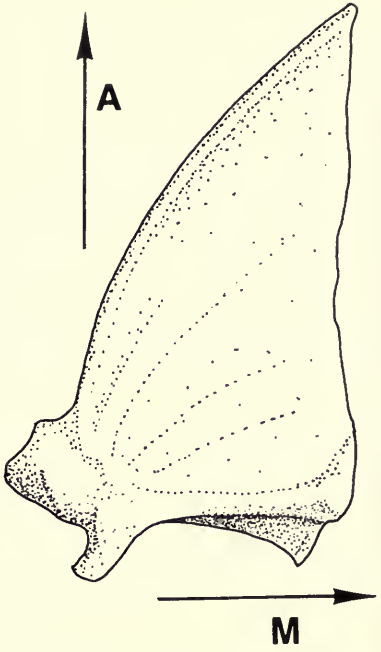


FIG. 9. *Apsopelix anglicus*, ventral view of right pelvic plate. A=anterior; M=medial.

toral ray and the first radial. The coracoid contacts the medial edge of the scapula posteriorly and the inner face of the cleithrum more anteriorly. Where the coracoid meets the scapula it forms a ridge continuous with the scapular ridge and supports the majority of the fin rays via the remaining radials.

The coracoids meet in the ventral midline to form a median ventral keel. This keel extends forward, but does not reach the cleithral symphysis. Posteriorly the keel extends back beyond the scapulacoracoid ridge. The mesocoracoid extends dorsally from its basal contact with the scapula and coracoid, forming an arch. Its dorsal end touches the medial surface of the cleithrum. There are four radials, the most medial being longest. They are simple struts, slightly expanded at their distal ends.

The prepelvic distance is about three-fourths of the standard length. Each pelvic fin is attached to a long, broad triangular pelvic bone (fig. 9) which extends anteriorly from the origin of the fin for a distance of about four abdominal vertebrae. There is a thickened ridge along the posterior edge of each pelvic bone. The two bones meet in a median symphysis along the ventral midline. This massive, broad pelvic bone is charactertistic of *Apsopelix*.

MEDIAN FINS (fig. 10): Of those specimens studied in which the whole fish is preserved, the ventral surface is exposed and the body twisted. The preservation of the median and caudal fins is poor. KU 309, KU 519, and SMM 7958, in which the dorsal fin is preserved, and UT 31051-7, in which the anal fin is preserved, show the best median fin preservation of the specimens examined in this study.

The dorsal fin is short, with about 11-12 rays, the longest being most anterior. The predorsal length is about 40 per cent of the standard length. The first dorsal ray is the longest and most robust.

The anal fin of *Apsopelix* is short and the preanal length is about four-fifths of the standard length. UT 31051-7 shows a few anal rays, but otherwise this fin is not known in *Apsopelix* apart from Cope's (1871) original description of AMNH 1602. Only the first anal ray is preserved in UT 31051-7, but examination of photos of AMNH 1602 show the anal fin with 10-12 rays.

The caudal fin is deeply forked, with a narrow base. The number of branched principal rays appears to be nine above and eight below, but such counts are difficult to obtain in the specimens examined and may be in error.

VERTEBRAL COLUMN AND CAUDAL SKELETON (fig. 10): There are about 40 preural centra; nearly 30 are abdominal. The centra are longer than deep, somewhat constricted at their centers, and pierced for passage of the notochord. Each centrum is marked by a single lateral ridge.

The neural arches of the anteriormost centra are autogenous, but otherwise they appear to be fused with the centra as are the haemal arches. Pleural ribs are associated with at least 20 centra, being absent from the first few vertebrae, but the nature of the rib articulations has not been preserved in the specimens examined. KU 18 shows numerous intermuscular bones. Above the pleural ribs are epipleural intermusculars which are forked anteriorly. Epipleurals also appear to be associated with haemal arches as far back as the 36th centrum. There appear to be short, straight epicentral intermusculars associated with the more anterior abdominal centra. Anteriorly forked epineural intermusculars are associated with the neural arches as far back as the 36th centrum.

The quality of caudal preservation in *Apsopelix* specimens is generally poor. It is fragmentary at best in the North American specimens, but Patterson and Rosen (1977) state that enough of it is visible in AMNH 8330 and in several British Museum specimens to

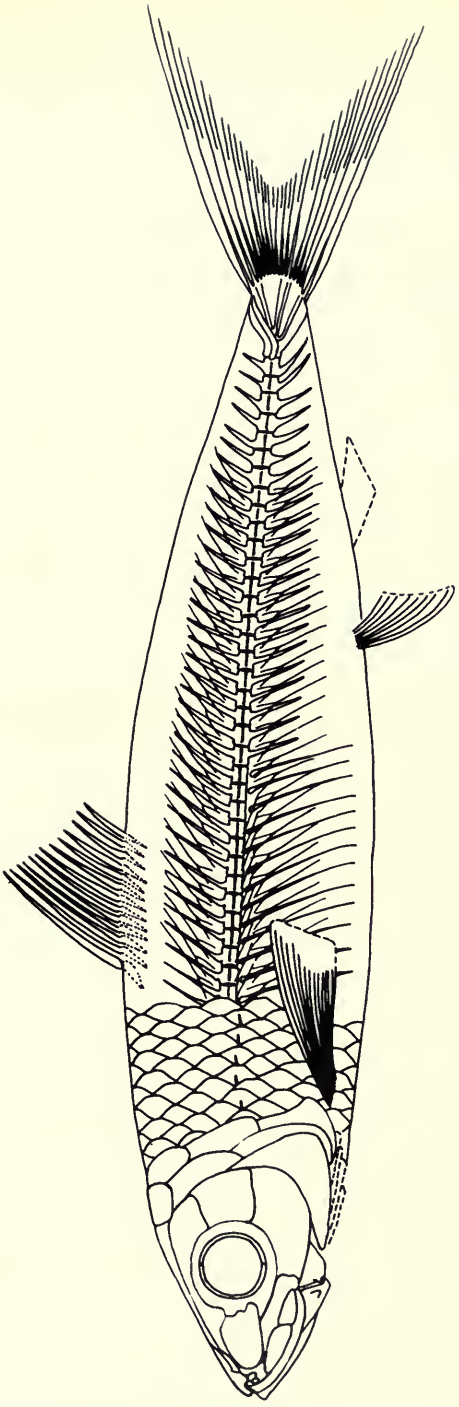

FIG. 10. *Apsopelix anglicus*, restoration of whole fish.

show that it is almost identical with that of *Crossognathus* (cf. Patterson and Rosen, 1977, fig. 21, p. 114), differing only in having the neural and haemal spines more strongly inclined and pressed together plus increased hypurostegy so that the proximal ends of the upper and lower principal rays almost meet. When compared with Patterson and Rosen's figure of the caudal skeleton of *Crossognathus*, the fragmentary caudal material from KU 309, KU 519, SMM 7958, and UT 31051-7 supports their conclusions.

In *Apsopelix* uroneurals 1 and 2 extend forward to the second preural centrum and the third uroneural extends forward to the first preural centrum. There are, in addition to these elongate uroneurals, a posterior set of shorter uroneurals, although the exact number cannot be determined in the specimens examined. There are more than six hypurals, but the exact number is uncertain. (There are nine hypurals in *Crossognathus.*). The first and second hypurals are fused or partly fused in all of the specimens examined for this study. The parhypural is fused to the first preural centrum. It and the haemal spines of $PU_1$ and $PU_3$ are broadly expanded. According to Patterson and Rosen (1977), there are caudal scutes present in *Crossognathus.* There is no evidence of caudal scutes in the North American specimens of *Apsopelix* examined in this study.

## DISCUSSION

A number of distinctive morphological features in *Apsopelix* (the large scales, antorbitals and pelvic bones, the form and proportion of the dermal upper jaw elements, the arrangement and ornamentation of the cranial roof bones) have facilitated identification and the proper assignment of specimens previously described as *Syllaemus, Pelycorapis, Leptichthys, Helmintholepis*, and *Paleoclupea.* However, these features along with nearly all others known in *Apsopelix* have little value as clues to the position of this genus among the teleostean fishes. It exhibits a host of characters primitive for teleosts, a few characters which seem to be unique to the genus *Apsopelix* (posteriorly directed fossa on the hyomandibular, premaxilla so reduced as to be nearly lost, basihyal with a pair of tooth plates along its lateral margins only, antorbital which nearly covers the ethmoid region, broadly expanded pelvic bone), and no suite of characters that unequivocally indicate to which major teleost group it is most closely related.

Of the major teleost groups, it is least likely that *Apsopelix's* relationships are to be sought among the euteleosts. It was placed

within the Percesoces[1] (Woodward, 1901) and Mugilidae (Stewart, 1900) on the mistaken assumption that the major element of the upper jaw was a premaxilla. *Apsopelix* shares none of the specializations unique to euteleosts (Patterson, 1970; Nelson, 1973a; Patterson and Rosen, 1977).

Certain features present in *Apsopelix* were thought by previous investigators (Stewart, 1900; Woodward, 1903, 1907; Jordan, 1923; Chabanaud, 1930; Berg, 1940) to be indicative of a relationship with clupeomorphs. These include: 1) laterally compressed body, 2) form and position of fins, 3) features associated with microphagous feeding (reduced dentition on the dermal jaws; short, deep lower jaw; curved maxilla with a flat articular head; large, mobile supramaxillae; long gill rakers).

Character 1 has proved to be either an artifact of preservation or an error of interpretation. Three-dimensionally preserved specimens of *Apsopelix* indicate that the body of this fish was ovoid or even pear-shaped in cross-section. This hypothesis is reinforced by the fact that the flattened specimens have been dorsoventrally compressed. A laterally compressed fish would be more likely to come to rest on its side and be preserved laterally compressed rather than dorsoventrally compressed as is the case in *Apsopelix.*

Character 2, the form and position of the fins, is present in *Apsopelix,* clupeids, and engraulids. It is also present in elopids, albulids, and (with the addition of the adipose fin) salmonids, osmerids, and other lower teleosts. Thus, the form and position of the fins is an adaptation to mode of life and found in several primitive teleost groups.

The third group of characters, those associated with microphagous feeding, form a functional complex to facilitate a feeding mode that developed a number of times in the course of teleost evolution. Among living teleosts the epibranchial organ, a structural adaptation to the microphagous feeding mode, has developed independently in at least four lineages of teleosts (Nelson, 1967). So it is reasonable to assume that the occurrence of this whole complex of characters, while valuable in reinforcing other evidence of a relationship, is not by itself sufficient to prove a connection between *Apsopelix* and clupeomorphs.

Until recently two characters previously unknown in *Apsopelix,* the presence of epipleural intermusculars and a ventral keel on the

[1]See footnote, p. 3

parasphenoid coupled with the extension of this bone posterior to the braincase, were also associated with clupeomorphs. Epipleural intermuscular bones are found at least in some osteoglossomorphs (Patterson, 1975) and the keeled parasphenoid is characteristic of North American specimens of *Pachyrhizodus*, a genus which Forey (1973b, 1977) associates with salmoniform euteleosts. Since these characters are not exclusive to clupeomorphs, it is unlikely that their presence in *Apsopelix* indicates clupeomorph affinities.

In summary, *Apsopelix* has been associated previously with clupeomorphs on the basis of characters which can be shown to have been erroneously described, plesiomorphic for teleosts, or convergent. Derived characters shared by clupeomorphs include a swim-bladder-ear connection involving penetration of the exoccipital and prootic, a temporal foramen between the frontal and parietal in the apex of the posttemporal fossa (Greenwood et al., 1966), supratemporal commissure associated with the supraoccipital (Patterson, 1970), a pleurostylar caudal skeleton (Greenwood, 1968; Gosline, 1971; but see Forey, 1975), fusion of the angular and articular with the exclusion of the retroarticular from the articular facet (Nelson, 1973b), and fusion of tooth plates Ib 1-3 and Cb 5 (Nelson, 1967). *Apsopelix* exhibits none of these characters so its relationships lie elsewhere.

Wenz (1965) and Romer (1966) assigned *Apsopelix* to the Elopoidei. *Apsopelix* shares a large number of primitive features with living members of the elopiform fishes (see Forey, 1973b, pp. 187-189), but these characters are found in members of all major teleost groups and are of no use in determining relationships. Patterson and Rosen (1977) cite four shared, derived characters for the cohort Elopomorpha: a leptocepholus larva, angular and retroarticular bones fused, rostral and prenasal ossicles, and a compound neural arch formed in cartilage over PU1 and U1. The first character is of no help in determining relationships of fossil fishes; the retroarticular is not fused with the angular in *Apsopelix*, and no rostral or prenasal ossicles are present in *Apsopelix*. The neural arches of the first ural and first preural centra are not preserved in the North American specimens of *Apsopelix* examined for this study, but in the similar *Crossognathus* there are separate neural arches over U1 and PU1.

Patterson and Rosen (1977) cite some resemblances between the posttemporal fossae of *Apsopelix* and those of megalopids, but state that in *Apsopelix* the condition is not precisely the same as in

recent megalopids. Other braincase similarities noted by Patterson and Rosen include the large myodome, shape of the intercalar, strongly ossified ethmoid region, and a deep pit in the lateral surface of the posterior part of the basioccipital suggesting the possibility of a simple otophysic connection.

None of these similarities is convincing. Differences in the formation of the posttemporal fossae between megalopids and *Apsopelix* (see Patterson and Rosen, 1977 p. 132) suggest convergence of this character. The enlarged myodome characteristic of *Apsopelix* and megalopids generally occurs in conjunction with a deep neurocranium and is not exclusive to megalopids. The intercalar of North American specimens of *Apsopelix* does not resemble that of Eocene megalopids (cf. figs. 3, 4 with Forey, 1973b, figs. 36, 37, 42, 43) as stated by Patterson and Rosen (1977). It is a proportionately smaller bone in *Apsopelix* without the posterior expansion present in Eocene megalopids. A heavily ossified mesethmoid is primitive for teleosts (Patterson, 1970). Finally, it seems likely that an otophysic connection per se must be looked upon as a primitive teleostean character (Greenwood, 1973).

In summary, there are no derived characters of elopomorphs shared with *Apsopelix*. Characters of the braincase shared by megalopids and *Apsopelix* can be more reasonably explained as convergent or primitive for teleosts, since the structure of the lower jaw and caudal skeleton of *Apsopelix* opposes elopomorph relationships. Thus, the probability of finding relationships of *Apsopelix* within the elopomorphs fades.

Part of the problem in comparing *Apsopelix* to the osteoglossomorphs is that this group is so diverse. Among those derived characters which are known in at least some osteoglossomorphs (see Greenwood et al., 1966, 1967; Greenwood, 1967, 1970, 1971, 1973; Nelson, 1968, 1969, 1972) there is only one which appears to be shared with *Apsopelix*. That character, fusion of Io 3 + 4 (Nelson, 1969), has yet to be firmly established as present in *Apsopelix*. Given that there is a fusion of Io 3 + 4 in *Apsopelix*, this character alone (found also in *Chanos* and cypriniformes) is not sufficient to indicate a relationship.

One similarity between *Apsopelix* and at least some fossil osteoglossomorphs could be the shape and disposition of the premaxilla. Judging from the relationship of the maxilla to the median ethmoid in *Apsopelix*, the premaxilla probably overlapped the anterior end of the maxilla and extended down over it to form the

anteriormost border of the upper jaw as in *Ichthyodectes ctenodon* and *Xiphactinus audax* (see Bardack, 1965, fig. 16, p. 58, fig. 9, p. 45). These three fishes also share an ossified malleolar process on the anterior end of the palatine, but this ossification appears to be a response to a functional need and is also present in some members of the elopiforms (Forey, 1973b).

This discussion has reviewed the four major teleost groups and argued against assigning *Apsopelix* to any one of these groups. The original hope of the authors was that more information concerning the morphology of *Apsopelix* would facilitate the discovery of its systematic relationships. The accumulation of this information has instead precipitated arguments against a systematic assignment of *Apsopelix* to any presently well-defined group.

In their analysis of the relationships of fossil and Recent teleosts, Patterson and Rosen (1977) place *Apsopelix* with *Crossognathus* as a nominal family incertae sedis within the group containing *Tharsis dubius* and extant teleosts.

That is, *Apsopelix* shares with *Tharsis dubius* the three features it exhibits which are synapomorphies with Recent teleosts,[1] but does not show any derived characters typical of a Recent teleost group. We agree with Patterson and Rosen (1977) and feel that it is preferable that *Apsopelix* be left incertae sedis rather than erroneously associated with a teleost group on the basis of convergent or plesiomorphous characters.

## GEOLOGIC AND GEOGRAPHIC RANGE

The oldest *Apsopelix* specimen known is a single fish from the Albian of France (Wenz, 1965). By Cenomanian time *Apsopelix* ranged throughout the North Temperate Euroamerican Region (Kauffman, 1973). It apparently did not enter other regions. Morphological features of *Apsopelix* remain constant throughout its geologic as well as geographic range. The Late Cretaceous specimens from the Western Interior do not differ significantly from the English, French (Patterson and Rosen, 1977), or Gulf Coast specimens. The morphological stability of *Apsopelix* in time supports the idea of punctuated equilibria (Eldridge and Gould, 1972; Gould and Eldrige, 1977), the concept of speciation as a rare event that punc-

[1]These three features are: loss of suborbital bones, presence of epipleural intermuscular bones, and uroneurals distributed in two series, i.e., the uppermost uroneurals overlap and lie at an angle to the longer anterior ones.

tuates a system in homeostatic equilibrium. Essentially, we have only the stable stage of evolution in this group.

The geographic distribution of *Apsopelix* coupled with the morphological similarity of individuals throughout its range is reasonable when viewed from the perspective of the configuration of continents and oceans in Cretaceous times (see Kauffman, 1973, fig. 2, p. 356). The greater proximity of the European and American continents during the Jurassic and Early Cretaceous combined with a similar biologic source area in the continuous north temperate seaway resulted in a close similarity of Northern European and North American bivalve faunas (Kauffman, 1973) and would support the similarity of Northern European and North American *Apsopelix*.

These fishes appear to have been specifically adapted to interior marine environments[1] of the north temperate realm, to have maintained a set of morphological adaptations to this type of environment through time, and to have become extinct with the disappearance of this type of environment.

## ABBREVIATIONS

| | |
|---|---|
| Ang | angular |
| apl | anterior pit line |
| Ao | antorbital |
| Art | articular |
| Asp | autosphenotic |
| Bsp | basisphenoid |
| Boc | basioccipital |
| Den | dentary |
| df | dilatator fossa |
| Dsp | dermosphenotic |
| Ecpt | ectopterygoid |
| Enpt | endopterygoid |
| Epo | epioccipital |
| Exo | exoccipital |
| fhm | hyomandibular facet |
| fhmVII | foramen for hyomandibular trunk of facial nerve |

[1]Specimens from Texas localities near the Western Interior/Gulf Atlantic Coast boundary are found with invertebrates and in sediments that are characteristic of interior marine rather than coastal shelf environments.

| | |
|---|---|
| fhv | foramen for head vein |
| fica | foramen for internal carotid artery |
| flap | fossa for levator arcus palatini |
| fmpVII | foramen for mandibular and preopercular branches of facial nerve |
| foa;fpalVII | foramen for orbitonasal artery; foramen for palatine branch of facial nerve |
| Fr | frontal |
| Hm | hyomandibular |
| Ic | intercalar |
| Io | infraorbital |
| IX | foramen for glossopharyngeal nerve |
| Le | lateral ethmoid |
| Me | median ethmoid |
| Mpt | metapterygoid |
| Mx | maxilla |
| Na | nasal |
| Op | operculum |
| Ors | orbitosphenoid |
| Pa | parietal |
| Pal | palatine |
| Par | parasphenoid |
| ple | process to lateral ethmoid |
| pme | process to median ethmoid |
| Pop | preoperculum |
| Pro | prootic |
| ptf | posttemporal fossa |
| Pto | pterotic |
| pts | pterosphenoid |
| Ptt | posttemporal |
| Qu | quadrate |
| Rart | retroarticular |
| Smx | supramaxilla |
| So | supraorbital |
| Soc | supraoccipital |
| Sop | suboperculum |
| stf | subtemporal fossa |
| Stt | supratemporal |
| Sy | symplectic |
| Vo | vomer |
| X | foramen for vagus nerve |

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